

# Phylogenetic System of the Tracheata (Mandibulata): on "Myriapoda" – Insecta interrelationships, phylogenetic age and primary ecological niches

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With 28 Figures

**Abstract:** The monophylum Tracheata, sister taxon of the Crustacea, is primarily characterized by details of the head capsule: loss of the appendages of metamere 3 (equivalent to the 2nd antennae in Crustacea); mandibles telognathic (hence without palp) – but not by the presence of tracheae. The Chilopoda form the sister taxon of all other tracheates. These also represent a monophyletic unit, called Labiophora. The Labiophora branched into the Progoneata (with Symphyla and Dignatha), and the Insecta (= Hexapoda). The traditional "Myriapoda" are regarded as a paraphyletic assemblage. Arguments are mainly derived from studies on functional morphology. According to the fossil record, the basic branching events happened in the Late Cambrium/Early Silurium. Non-predators presumably fed primarily on fungi, green algae etc. by penetrating or by damaging cell walls. Accordingly, early tracheates were remarkably small animals. Their primary food niche coincides with various independent origins of semi-entognathy (e.g., in Pauropoda, Pselaphognatha and Carboniferous Diplura), and with the entognathous condition in one of two basic branches of the Insecta (Entognatha) as well as in the Colobognatha (Diplopoda). In principle, only representatives of the Chilognatha (among diplopods) and of many subtaxa of the Pterygota (among insects) successfully entered new food niches; this was correlated with an increase in body size of such non-predacious animals. In the majority of the higher taxa (e.g., Symphyla, Pauropoda, Pselaphognatha and Entognatha), however, the original small size of approximately 1 to 2 mm body length was more or less maintained. The elongation theory is confirmed for high segmented chilopods and diplopods.

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## A. Introduction

The monophyletic origin of the Tracheata (Fig. 1) has never been seriously questioned (e.g., BOUDREAUX 1979, 1987; HENNIG 1969, 1981). The presence of tracheae is a characteristic of the group but not necessarily an autapomorphy of the taxon. There is evidence that tracheae have evolved in parallel but independently in various tracheate subtaxa. Nevertheless, there are various other sound autapomorphies (Fig. 2). This is especially true for the lack of appendages of the 3rd metamere of the head capsule. In tracheates, this metamere is commonly called the "intercalary segment". It corresponds to the metamere that bears the second antennae in Crustacea.

There was and still is much controversy over the phylogenetic relationships between the major subtaxa of the Tracheata (see, e.g., DOHLE 1980; HOPKIN & READ 1992: 16). This especially concerns the historical and persisting dispute whether the Myriapoda in the wider, traditional sense form a monophyletic unit and should be regarded as the adelphotaxon to the Insecta (HENNIG 1969: 81–94). The alternative would be that only a subtaxon of the so-called Myriapoda forms the sister group of the insects (SNODGRASS, e.g., 1938).

BALLARD et al. (1992) tried to analyse arthropod relationships on the basis of 12S ribosomal RNA sequences. They concluded (their Fig. 3A) that myriapods (millipedes *and* centipedes) form the sister group of all other assemblages (i.e., onychophorans, chelicerates, crustaceans, and hexapods) (sic!). Unfortunately, they analyzed three chilopod species for their study, but the conclusion also related to diplopods – without any reservations. We will not comment further on this.

WHEELER et al. (1993) compared ribosomal and ubiquitin (sic!) coding sequence data with morphological characters. Their consensus diagram derived from molecular sequence data (: 13) suggests, e.g., a sister group relationship between the Crustacea and the Odonata (!). A final consensus cladogram derived from both molecular and morphological data goes no further than a phylogenetic tree (: 17) proposed 44 years ago by SNODGRASS (1938).

It was POCOCK (1893) who was the first to abandon the myriapoda in toto. He proposed classifying the tracheates into Progoneata and Opisthgoneata. The opisthgoneates were certainly based on a plesiomorphic feature; they comprised all non-progoneates among the Tracheata.

MANTON's ideas (e.g., 1969, 1977) should not be regarded as reconstructions of phylogenetic relationships in a strict sense (Fig. 3).

KAESTNER (1963) maintained a "class" called Myriapoda. He classified this assemblage into three divisions of equal rank: Chilopoda, Dignatha (with Diplopoda + Pauropoda) and Trignatha (with the Symphyla). He believed that the maxillae II were completely lacking in all the Dignatha. This led him to the conclusion that the head capsule was one metamere shorter in Dignatha than in all other tracheates. At the same time, he assumed closer relationships between Symphyla and Insecta (= Hexapoda), according to SNODGRASS' Labiata (1938). So he indirectly questioned the concept of a "class Myriapoda".

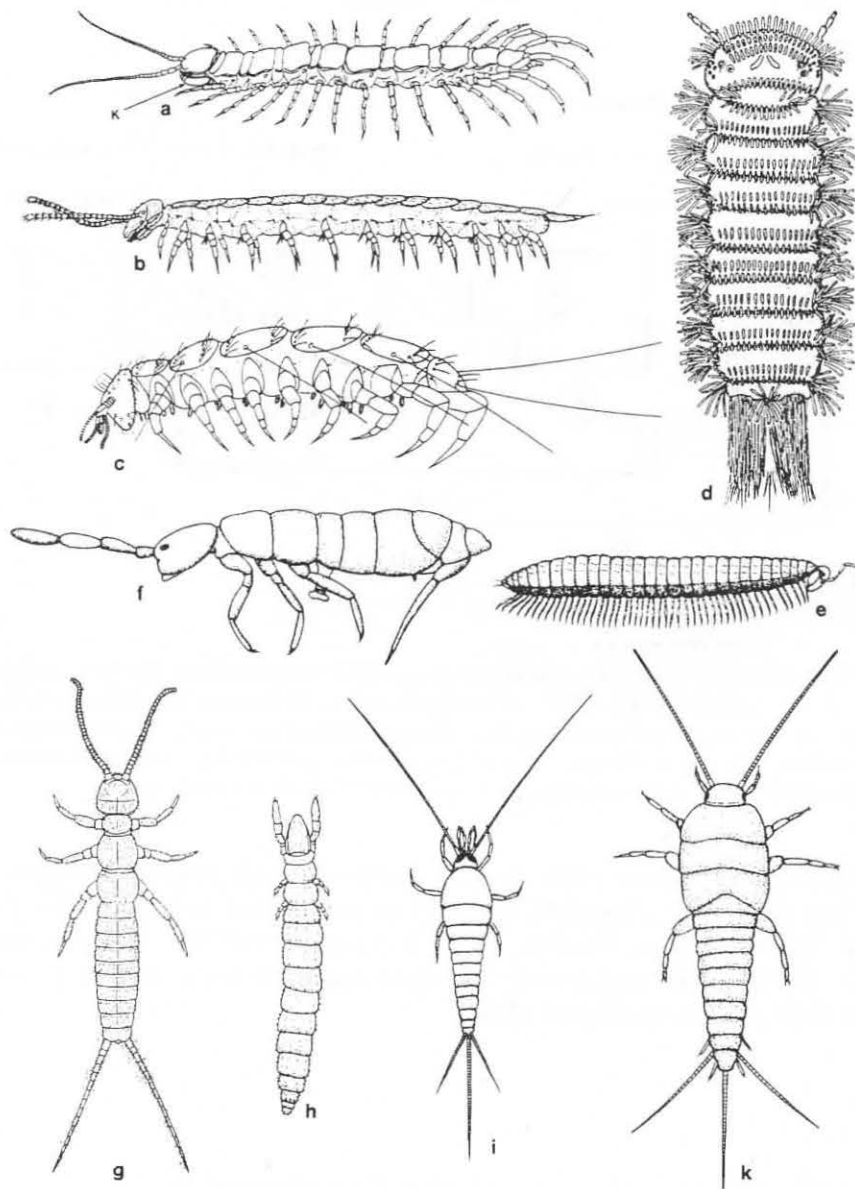


Fig. 1: Representatives of higher subtaxa of the Tracheata. - a) Chilopoda (*Lithobius*); b) Symphyla (*Scutigera*); c) Pauropoda (*Allopaupopus*); d) Diplopoda-Pselaphognatha (*Polyxenus*); e) Diplopoda-Chilognatha (*Chordeuma*); f) Collembola (*Isotoma*); g) Diplura (*Campodea*); h) Protura (*Sinentomon*); i) Archaeognatha (*Machilis*); k) Zygentoma (*Lepisma*). - After various authors; from EISENBEIS & WICHARD (1985).

BOUDREAUX also maintained a class called "Myriapoda" (1979: 578-583, 1987: 120-122). He distinguished two subtaxa, the Collifera [= Dignatha] (with Pauropoda + Diplopoda) and the Atelopoda (with Symphyla + Chilopoda). According to BOUDREAUX, there is a sister-group relationship between "Myriapoda" and Insecta.

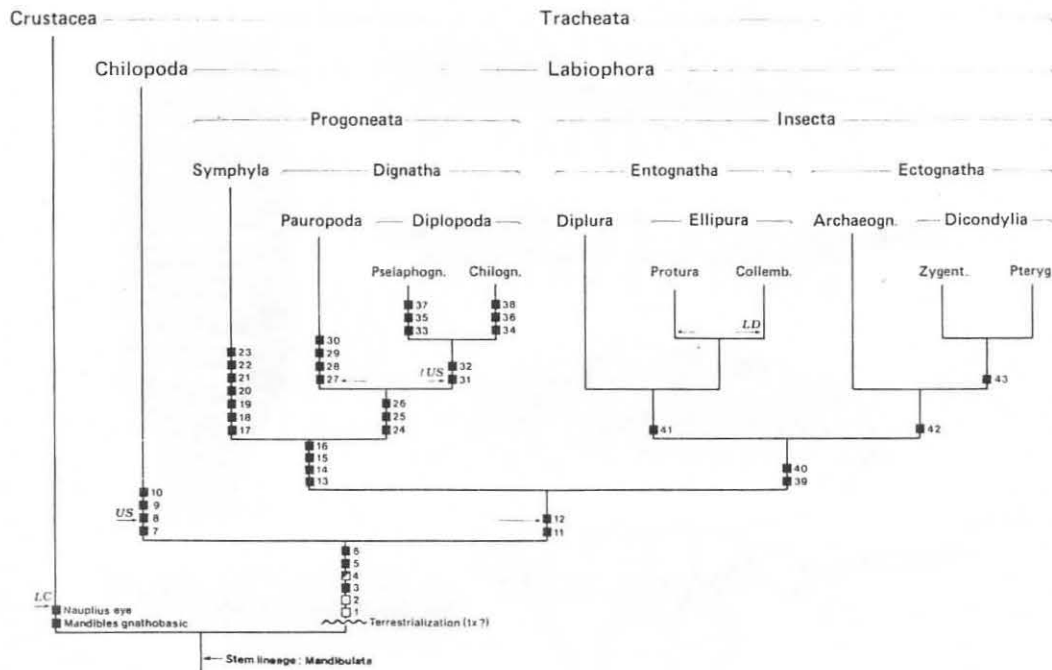


Fig. 2: Adelphotaxon and phylogenetic relationships of higher subtaxa of the Tracheata: argumentation scheme. - Arrows indicate the age of the earliest fossils hitherto known; an equivalent age is assigned to those sister taxa that are not yet represented by corresponding fossil materials. LC: Lower Cambrian; LD: Lower Devonian; US: Upper Silurian. - Closed boxes indicate apomorphies, open boxes plesiomorphies. Numbers correspond with numbered sequence of discussion of characters in the text.

The purpose of the present paper is (i) to evaluate already known characters, (ii) to present new data and arguments, and (iii) to put an end to a confusion that has persisted for more than hundred years (Pocock 1893). We further attempt to determine the minimum phylogenetic age of the major tracheate subtaxa and to derive ideas on their primary ecological niches.

## B. Head and mouthparts of the Euarthropoda

Uncertainties briefly mentioned in the Introduction are primarily due to

- the lack of knowledge (various authors, including BOUDREAUX 1987: 121, 129) of the real sequence and number of metameres included into the euarthropodean head capsule;
- various differing misinterpretations of the gnathochilarium and of its components (DOHLE 1964, 1980; ENGHOFF 1990: 7), a structure thought to be present in all diplopods and in the Pauropoda.

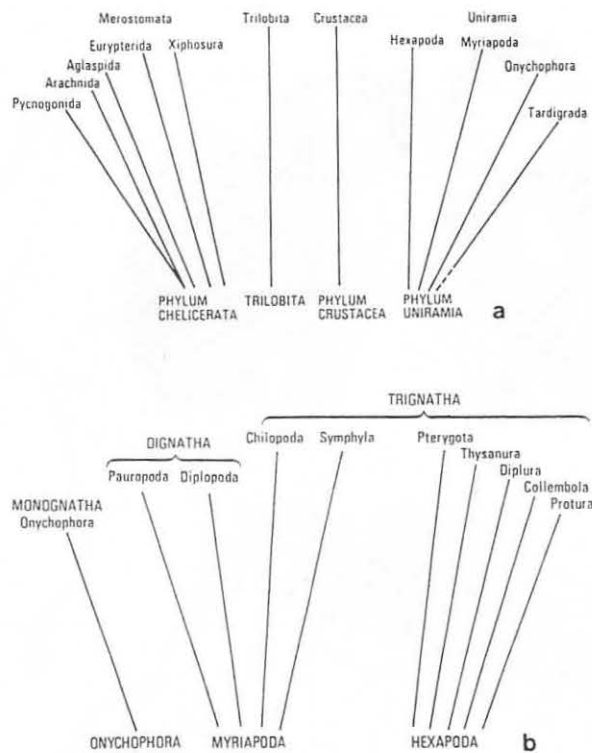


Fig. 3: MANTON's ideas. – a) Grouping of higher taxa within the Arthropoda; b) assumed relationships within the "Uniramia". – From MANTON (1977), Fig. 6.1, 6.12.

## I. Metameres composing the head capsule

The head capsule of the Tracheata and even of the Euarthropoda as a whole (early fossils excluded; see WALOSSEK 1993) is composed of an acron (homologous to the prostomium in polychaetes) and 6 successive metameres. This has been definitively demonstrated by various authors (see, e.g., LAUTERBACH, 1980a, b). Consequently, the previous assumption is now excluded that the dignathean head included only 5, and not 6, metameres. What can be observed is a secondary and only superficial separation of the last (6th) metamere by a fine dorsal suture in the Pauropoda (TIEGS 1947: 304) and at least in some Pselaphognatha among diplopods (ATTEMS 1926: 109).

## II. Homology of the components of the gnathochilarium

The homology of various components of the gnathochilarium of the Chilognatha (among diplopods, Fig. 4) and of the so-called gnathochilarium of the Pauropoda (Fig. 16) has been treated by various authors, with extremely divergent conclusions (for details see HILKEN 1992; HILKEN & KRAUS 1994: 34). There was and still is basic dichotomy of opinion as to whether the gnathochilarium should be understood as a

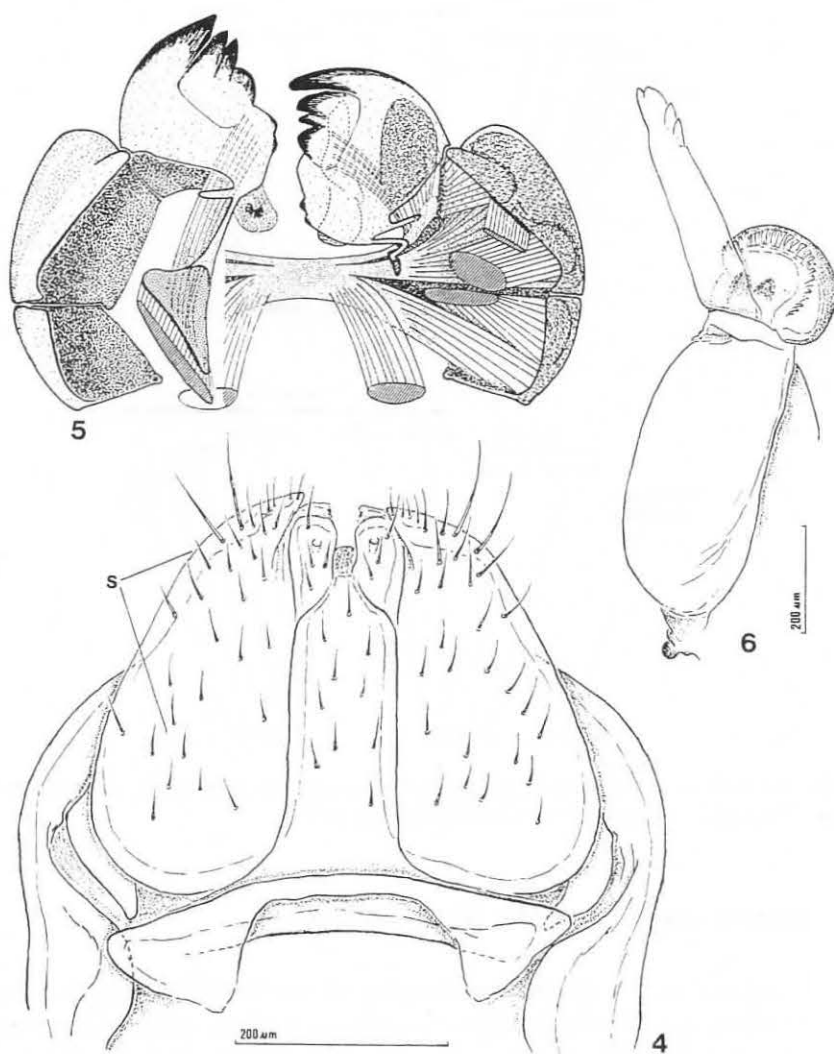


Fig. 4-6: *Platydesmus* sp. (Diplopoda, Colobognatha) Gnathochilarium. - 5) *Poratophilus* (Diplopoda, Chilognatha), Mandibles, including musculature. - From MANTON (1977), Fig 3.17; 6) *Lepismachilis targionii* (GRASSI, 1887) (Hexapoda, Archaeognatha), mandible.

complex composite made up of the first *and* second maxillae or should be traced back only to the first maxillae (perhaps with vestiges of the second maxillae at its base?). The latter assumption presupposes that the maxillae II were almost completely reduced.

It was VERHOEFF (e.g., 1911-14: 304)<sup>1</sup>, in particular, who insisted that the gnathochilarium was composed of two pairs of appendages. Unfortunately, however, lie

<sup>1</sup> We refer to VERHOEFF's "*Diplopoden Deutschlands*", as this work is much closer to the original research of this author than his monographic treatment in BRONN's "*Klassen und Ordnungen des Tierreichs*" (VERHOEFF 1926-32).

interpreted the median components ("lamellae linguales") as part of the maxillae I, and the lateral elements ("stipites") as the maxillae II (see below).

In principle, this interpretation is in conflict with observations and conclusions drawn from the ontogeny of various representatives of the Diplopoda-Chilognatha (see DOHLE, e.g., 1980). He found that the *anlagen* of the mandibles were followed by only one pair of *anlagen* of appendages, whereas the next metamere did not show any buds of appendages at all. These findings were directly interpreted as a confirmation for the previously assumed homology of the gnathochilarium as a complex formed solely by the first maxillae. Hence, the adjoining metamere was regarded as representing the segment of the second maxillae - without appendages. DOHLE had not (1980), and has still not, made any attempt to propose homologies for the components of the "complete" gnathochilarium in the Diplopoda-Chilognatha.

On the other hand, PFLUGFELDER (1932) reported that he had seen *anlagen* of appendages on the segment of the second maxillae. He studied the embryology of a conspicuously large diplopod, *Platyrhacus amauros* ATTEMS, 1897 (Chilognatha, Polydesmoidea).

As stated above, nearly all previous studies were based on data derived from the ontogeny and from structural details of the head capsule of postembryonic or adult stages only of the Chilognatha among diplopods. Hence, the total spectrum of diversity was notoriously neglected. This means that (1) investigations on the mouthparts of the Pselaphognatha, the second subtaxon of the Diplopoda, and (2) a new evaluation of the appendages of the head capsule in the Pauropoda are needed.

### 1. *Pselaphognatha*

The mouthparts of a representative of the Pselaphognatha (*Polyxenus lagurus* (LINNÉ, 1758)) were first studied in any detail by CARPENTER (1905). *P. lagurus* (Fig. 10-11, 14-15 see p. 18-19) shows paired, very conspicuous appendages (*T*), equipped with a certain number of prominent sensillae. Vestiges of articulations are discernible (Fig. 14, *G*). There are two short segments at the base of each of these appendages. They presumably represent a (basal) coxal element followed distally by the trochanter. This pair of appendages inserts on a broad transverse plate (*IP*), apparently a sternite. The whole structure described here is interpreted as the second maxillae, and the leg-like components as their telopodites. We cannot see any possible alternative explanation. It should be noted that the telopodites can be shortened to varying degrees or even reduced in representatives of other genera (e.g., *Monographis*, *Alloproctus*, *Lophoproctus*; see CONDÉ & JAQUEMIN 1962, 1963). Presumably, this is a parallelism to the origin of the paired interior "Taster" at the anterior border of the lamellae linguales in the Chilognatha.

Another pair of appendages (Fig. 4, *S*) has a lateral and somewhat more anterior location, i.e., closer to the mandibles than the second maxillae. These appendages also show vestiges of earlier segmentation (Fig. 14, *G*). There is a membranous connection between them and the basal plate of the maxillae II. We suggest that the main function of these appendages is to close the oral cavity laterally; that is to say,



to tighten the gap between the (anterior) mandibles and the (posterior) second maxillae. The opening of the "Putzdrüse" (Fig. 14, *P*) is clearly discernible in the distal part of the membrane which connects the lateral pieces described here with the maxillae II. According to the position and structural details of the pair of appendages in question, they are interpreted as the first maxillae. We cannot see any possible alternative explanation. The possibility of derivation from parts of the hypopharynx is excluded.

## 2. Pauropoda

The results reported thus far and the postulated homologies are in good agreement with details of the mouthparts in Pauropoda. These tiny animals were thoroughly studied by TIEGS (1947). But we cannot agree with his interpretation (: 182). The unpaired structure that he called the "intermaxillary plate" (Fig. 18) obviously represents the maxillae II (*Mx II*). There are also paired lateral structures. They are composed of various segments (TIEGS called them *cardo*, *stipes*, and *lacinia*). We recognize these appendages as the first maxillae (*Mx I*). This homology is supported by the special position of these mouthparts. It was TIEGS who already pointed out that the distal components of the maxillae I are located behind the mandibles and in front of the plate representing the maxillae II (see TIEGS 1947, Fig. 2). Further, we expressly refer to his drawing of the anterior part of an "advanced pupa" of *Pauropus silvaticus* (see TIEGS 1947, Pl. 3 Fig. 33A). We can confirm this observation. Representatives of the Hexamerocerata (a group sharing more plesiomorphies than any other pauropod taxon) also have the first maxillae behind the large, subdivided (!) mandibles but in front of the second maxillae (Fig. 16-17). The same is true for Brachypauropodidae (Fig. 18).

DOHLE (1980: 88) remarked on the superlinguae, which are paired derivatives of the hypopharynx. He noted that these structures need not be regarded as "Extremitäten eines eigenen Segments" [appendages of a separate segment]. This is unquestionably true, but we expressly state that the mouthparts regarded here as representing the maxillae II are - on the basis of their position and segmentation - completely different from superlinguae (see also TIEGS 1940, Fig. 18; 1947, Fig. 2E, F).

## 3. Conclusions

a) The present analysis demonstrates that both maxillae I and II are present in the Diplopoda and in the Pauropoda, i.e., in the Dignatha (= Collifera BOUDREAUX, 1979). This higher taxon can no longer be characterized by such statements as "maxillae II absent" or "segment of 2nd maxillae not included into the head capsule". Hence, the 'perfect' gnathochilarium of the Diplopoda-Chilognatha is composed of the lateral maxillae I (= "stipites") and the median maxillae II (= lamellae linguales). This homology is confirmed by a detailed study of the gnathochilaria of adult representatives of the Chilognatha (HILKEN & KRAUS 1994). In chilognath diplopods, both pairs of appendages, first and second maxillae, insert secondarily at the same level; they are tightly folded together, but remain much more flexible than previously



expected. This clarification makes the mouthparts of the Dignatha comparable with those of the third progoneate taxon, the Symphyla. Astonishingly, never at any time has the regular sequence of mouthparts (mandibles, maxillae I. and maxillae II) in symphyleans been questioned (Fig. 8-9).

b) Previous confusion was primarily caused by conclusions based on embryological data *as such* (see DOHLE 1964, 1980). Can one really expect that basic structures present in postembryonic instars are always discernible during the course of embryonic development? This would be plainly wrong. Accelerations and also retardations are possible in the realization of structures (for details see FUTUYMA 1986: 303; GOULD 1977: 209-245). In diplopods, two different authors have observed retardations of this kind. KRAUS (1990) was able to demonstrate that their so-called thoracic segments

are diplosomites, even though this was not observed in embryonic stages by DOHLE (1964, 1980). ENGHOFF (1993) discovered the phenomenon of haplopody in the Cambalopsidae (Spirostreptida): early postembryonic stadia may have only one pair of legs on each leg-bearing ring. The normal diplopodous condition is achieved at the moult to the IVth (?) stadium.

Innervation patterns *as such* are another feature that should not be overestimated without sufficient understanding of functional-structural correlations. This aspect is expressly mentioned because the gnathochilarium is innervated by one single ganglion (FECHTER 1961). Previous authors (e.g., DOHLE 1980) believed that this feature could indicate its homology with only one pair of appendages, the first maxillae.

c) The so-called gnathochilarium of the Pselaphognatha and of the Pauropoda proves to be a fiction: see DOHLE's Figs. 10 and 12 (1980).

## C. Phylogenetic relationships

We follow HENNIG's original terminology (1950, 1969, 1982) and call the phylogenetic tree in Fig. 2 an *argumentation scheme* rather than a cladogram. The reason for this distinction lies in the fact that cladograms in the strict sense are commonly produced by computer programs. Pattern cladistics works with little or no reference to any kind of *a priori* considerations on the origin, the functional morphological significance, or the direction of transformation ("Leserichtungs-Kriterien") of characters.

With due consideration for the insight obtained in chapter B, we argue as follows:

### I. Ground pattern of the Tracheata (= Antennata)

(1) Arthropodia. - Various taxa of crustaceans show so-called turgor appendages (term and function do not coincide). Examples of such taxa are the Cephalocarida, the Branchiopoda, and the thoracopods in Phyllocarida (Leptostraca). Without discussing the ground pattern of euarthropodean limbs here, the acquisition of arthropodia

("Stabbeine") was a prerequisite for a transition to terrestrial life (LAUTERBACH 1980a: 147). Apparently, these appendages were uniramous (*sensu* MANTON 1977), with at least 7 podomeres. Arthropodia form one of the most basic acquisitions of the arthropods as a whole (see WALOSSEK 1993); hence they were already present in the ground pattern of the tracheates.

Differences in segmentation and articulation patterns of the limbs in different major groups (see MANTON 1977: 255ff.) could indicate that evolutionary pathways were different. This view correlates with a remarkable non-uniformity of tracheal systems, including different positions of the spiracles (= stigmata) in the Notostigmophora, in all other chilopods, in the Dignatha (see discussion of character 24), and in insects. It therefore remains uncertain whether the transition to terrestrial life happened once or more than once in the Tracheata. The single water surface indicated at the bottom of Fig. 2 may be most parsimonious but wrong.

(2) Maxillae II. – There are strong arguments for supposing that the second maxillae were leg-like in the ground pattern not only of the tracheates. This has been maintained as a plesiomorphic feature in the Chilopoda (most conspicuously in the Notostigmophora; see Fig. 24) and also in the Pselaphognatha (Fig. 10, 14). As the same character stage forms part of the ground pattern of the Crustacea (see, e.g., the second maxillae of the Cephalocarida) (MOORE 1969), we conclude that leg-like second maxillae were already present in the stem lineage of the Mandibulata as a whole.

(3) Mandibles. – Telognathic mandibles ("Ganzbein-Mandibeln", "gegliederte Mandibeln"), of course without palps (Fig. 5–6, 17, 22), were regarded as an autapomorphy of the Tracheata (MANTON, e.g., 1977; for a critical discussion see DOHLE, 1980: 83ff.; GIACCHI 1988). On the other hand, there is no doubt that the mandibles of the Crustacea (*with* palps) are gnathobasic (LAUTERBACH 1972, 1980a). This would imply the conclusion that both tracheates and crustaceans transformed the appendages of the 4th metamere of the head capsule into mandibles – but in different ways. The case for regarding the presence of mandibles (*as such*) as an autapomorphy of a monophylum Mandibulata would hence be weakened.

An alternative view was advocated especially by LAUTERBACH (1972, 1980a: 146). He argued that all mandibles, including those of the Tracheata, are gnathobasic. This would imply that all other distal segments (corresponding to the mandibular palps in crustaceans) were already reduced in the tracheate stem lineage.

Should this be true, it would involve us in severe difficulties. How could one explain the parallelism of a secondary subdivision of gnathobasic mandibles into different movable components in different (!) phylogenetic lineages? We refer to subdivided mandibles in the Chilopoda (Fig. 22), in Pauropoda (Fig. 16–17), and in Diplopoda (Fig. 5), but also to vestiges of podomere borders in the Archaeognatha (Fig. 6); mention must also be made of the tripartite mandibles in *Dinjapyx* (Diplura) (MARCUS 1951).

In contrast to LAUTERBACH's view, the interpretation of the tracheate mandible as telognathic is not only supported by the morphological data just mentioned but also by arguments derived from functional morphology: as these mouthparts are composed of several parts, they may function like the arm of a dragline excavator, including a terminal shovel. Chilopod mandibles (Fig. 22), very recognizably in *Lithobius*, and also in diplopods (Fig. 5; see MANTON 1977: 102), correspond very well to this principle, longitudinal muscles included (corresponding to the draglines of the excavator). – We conclude that it is a feature of the tracheate ground pattern that the mandibles alone function as transporting device for food into the mouth cavity and towards the pharynx. It is not surprising at all that precisely this part of the foregut is quipped with pharynx dilators (see, e.g., WEIDNER 1982: 262–266). A special mode of complex cooperation of mandibles and first maxillae evolved in the Ectognatha. This is functionally correlated with the acquisition of dicondylic mandibles: In the Dicondylia, it is the pair of first maxillae that hauls the food into the mouth cavity (see, e.g., KAESTNER 1972: 92–93, 96). As one component of the original double function of the mandibles (hauling) was taken over by the first maxillae, the acquisition of secondarily fused, homogeneous mandibles is not at all surprising<sup>2</sup>.

In conclusion, we think that origin, function, and constructional changes of the feeding mechanisms within the Tracheata can only be consistently explained by assuming that telognathic mandibles were part of the ground pattern.

The alternative assumption – gnathobasic mandibles – would cause extreme difficulties in producing a model for primary feeding mechanisms. Further, a model explaining the fragmentation of primarily unique mandibles into movable components would be needed. Moreover, it would be necessary to accept that this trend towards a supposed fragmentation (this then would be still traceable in Diplura, Archaeognatha and even [personal observation] in the Zygentoma) was inverted in the Pterygota – in contradiction to DOLLO's rule. Altogether, so many complicated assumptions would be necessary that this idea seems about as substantial as a house of cards.

(4) Tarsal claws. – HENNIG (1969: 89, 1981) assumed that paired tarsal claws formed part of the ground pattern of the Tracheata. This would mean that they were maintained in the Symphyla, Pauropoda, Diplura and in all Ectognatha. But only a low value is assigned to the character "tarsal claws paired". The reason for this view is that a reliable discrimination is not yet possible between paired claws and unpaired main claws with one (Fig. 7 a–b) or two accessory claws (Fig. 7 c). Therefore, it is not yet possible at present to decide whether the alternative assumption – unpaired claws in the tracheate ground pattern – could be more probable. Perhaps paired claws originated more than once by way of an increase in the number of accessory claws.

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<sup>2</sup> Representatives of the Dicondylia (as well as some Crustacea) sometimes show a mandibular appendix called the lacinia mobilis (MANTON 1977: 86; WEIDNER 1982: 113, 116). Homology and function of these structures remain uncertain.

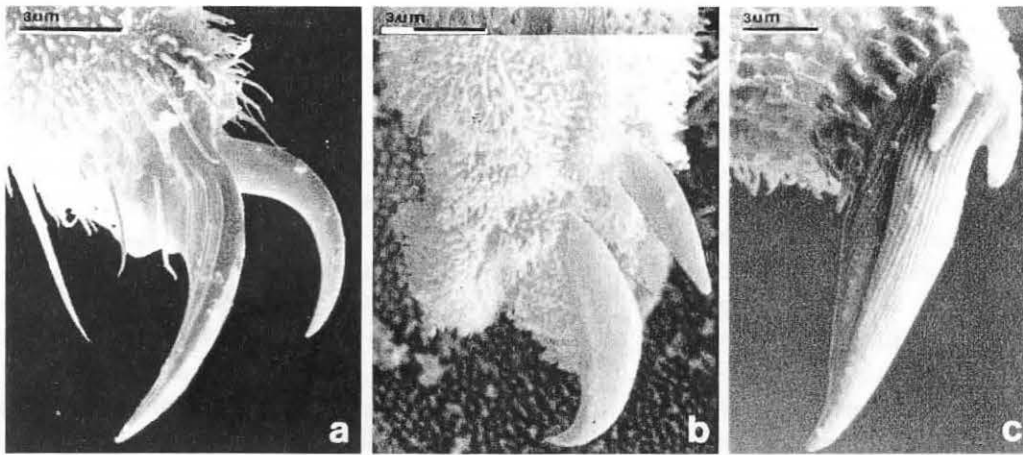


Fig. 7: Tarsal claws. – a) Symphyla gen. sp.; b) Pauropoda (Brachypauropodidae) gen. sp.); c) *Polyxenus lagurus* (Diplopoda, Pselaphognatha).

(5) Intercalary segment. – The term intercalary segment refers to the loss of the appendages of the 3rd metamere of the head capsule, homologous to the antennae II in Crustacea (= “antenna” of crustaceologists).

(6) Loss of midgut glands. – Midgut glands are lacking in all Tracheata. This may well be a sound autapomorphy for the taxon as a whole. Part of the function of these glands has been taken over by malpighian tubules. They are present in all tracheates. The most parsimonious assumption would be to regard a character “malpighian tubules present” as another autapomorphy. But we hesitate to embrace this conclusion as only very few ultrastructural and functional studies on the tubules are available (e.g., HOPKIN & READ 1989; WENNING 1989; WENNING et al. 1991). They are insufficient for comparative approaches and, hence, for decisions on homology. Superficially, malpighian tubules differ considerably in shape in different tracheate subgroups.

## II. Chilopoda as the adelphotaxon to all other Tracheata

BOUDREAUX (1979, 1987) classified the progoneate Symphyla as the adelphotaxon of the opisthogoneate Chilopoda. His main arguments for this supposed relationship were based on erroneous concepts: BOUDREAUX believed in the homology between the first postcephalic metamere of the Dignatha (= Collifera BOUDREAUX, 1979) and the metamere of the second maxillae in Symphyla + Chilopoda (= Atelopoda BOUDREAUX, 1979). This would imply that the head capsule in BOUDREAUX' Atelopoda included one metamere more than in the Dignatha (= Collifera). This argumentation is not longer valid (see section B II). The Atelopoda concept is further improbable as it would mean accepting that progoneaty evolved twice, separately in the Symphyla *and* in the Dignatha.

Our arguments are as follows:

(7) Maxillipedes. – The monophyly of the primarily predacious Chilopoda is confirmed by the transformation of the appendages of the first postcephalic metamere into maxillipedes (“Kieferfüsse”) (Fig. 1a, *K*).

(8) Ventral border of the mouth cavity. – In chilopods, the mouth cavity is ventrally (or posteriorly, respectively) bordered by the maxillae I (*Mx I*). In principle, their shape is dish-shaped, not flat (Fig. 21, see p. 21). Short and compact telopodites (Fig. 23, 25, *T*) form the lateral, and paired projections at the anterior border of the coxosternite form the median components of the “dish”. We expressly stress the presence of a telopodite (“palp”) composed of several podomeres.

As all other tracheates, chilopods are trignathous. But they are dignathous from the functional point of view.

(9) Stemmata. – In chilopods, the original compound eyes present in the ground pattern of the Tracheata were transformed into stemmata. The presence of prominent pseudocompound eyes in the Notostigmophora (= Scutigeromorpha) is secondary and hence does not contradict this statement. Details of the structure of these eyes differ considerably from regular compound eyes (for details see PAULUS 1979: 321–325, 367).

– See characters (33), (34).

Compound eyes were reduced several times in various taxa of the Euarthropoda and also in tracheates. Stemmata composed by the light-sensitive cells of several or even many (original) ommatidia are superficially covered by a syncornea. We refer to the Diplopoda-Chilognatha (see HOPKIN & READ 1992: 90 for review) and, e.g., to caterpillars and larvae in beetles.

(10) Median eyes. – Median eyes (“ocelli”) were reduced in all chilopods.

Reduction of the median eyes also happened independently in many tracheate groups, insects included.

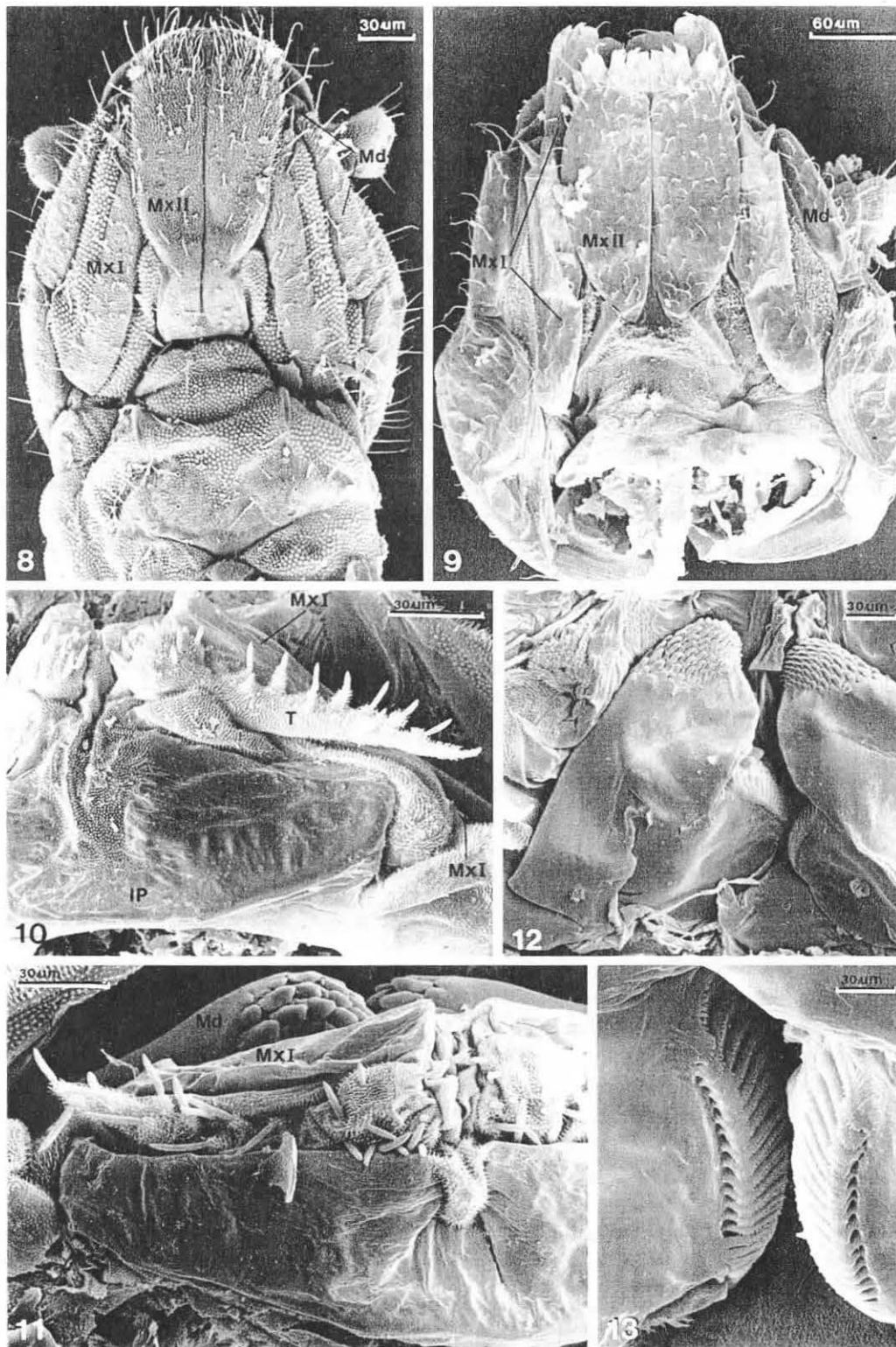
### III. Adelphotaxon of the Chilopoda: Labiophora nov.

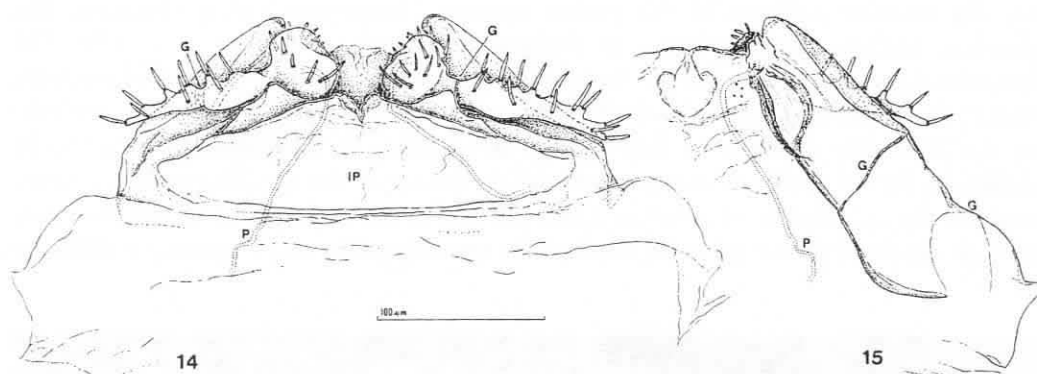
(= Progoneata + Insecta [= Hexapoda])<sup>3</sup>

(11) Coxal vesicles, styli. – We think that the presence of coxal vesicles and also of styli forms part of the ground pattern of the Labiophora. There is no reliable indication that structures of this kind might once have been present in chilopods. This view is supported by the fact that chilopods have quite different organs for the same function: their coxal pores (“Hüftporen”) are regarded as a functional analogon to coxal vesicles (for details see ROSENBERG 1982, 1983; LITTLEWOOD, 1991). The terminal bivalvular structures typical for *Craterostigma* (see DOHLE 1990, Fig. 9–10) are nothing but coxal pores (BORUCKI, pers. comm.). – HEYMONS (1901: 53–54, 66) referred to what

<sup>3</sup> Labiata SNODGRASS, 1938 (= Atelopoda BOUDREAUX, 1979) was originally introduced as the name for a hypothetical taxon comprising the Symphyla and the Insecta. Both designations, Labiata and Atelopoda, remained fairly unused. They do not refer to a monophyletic unit. Maintaining Labiata by broadening its scope (by including all other non-chilopods among tracheates) would have caused permanent confusion. Further, Labiata was in use in botany. It is for such reasons that we introduce the name Labiophora.







Figs. 14-15: *Polyxenus lagurus* (Diplopoda, Pselaphognatha). - 14) Maxillae I and II ("Gnathochilarium") from behind (= outside); 15) anterior view (= ventral border of mouth cavity).

he called "Coxalfortsätze" in late developmental stages of *Scolopendra dalmatica* C.L. KOCH, 1847, but their homology with styli seems to be highly questionable.

DOHLE (1980: 86) pointed out that the position of coxal vesicles is not absolutely identical in different taxa. This could be, but is not necessarily an argument against our view.

(12) Maxillary plate. - Whereas the ventral (or posterior, respectively) side of the mouth cavity is bordered by the first maxillae in chilopods, the same function is performed by basal parts of the maxillae II in the Labiophora. According to our clarification of the composition of the gnathochilarium in the Chilognatha and comparable structures in the Pselaphognatha and Pauropoda, these components, i.e., both maxillae, are also present in the Dignatha (Fig. 4, 8-10, 18).

(00) Dorsal organs; superlinguae. - Dorsal organs are known to occur in representatives of the Symphyla, Diplura and Collembola during the course of ontogeny. Structures somewhat different in detail but comparable have also been found in some Zygentoma, Pauropoda and also Chilopoda; see DOHLE (1980: 88) for a critical discussion. Dorsal organs may, then, be another potential autapomorphy of the Labiophora but we hesitate at present to include this feature in our argumentation scheme. - The same is true with regard to the presence of superlinguae (see DOHLE 1980: 88). Details of their structure and function remain insufficiently known.

## 1. Progoneata

(13) Progoneaty. - Various authors, including VERHOEFF (e.g., 1909-1914: 8-30) followed Pocock (1893) in recognizing a taxon Progoneata. This grouping was based

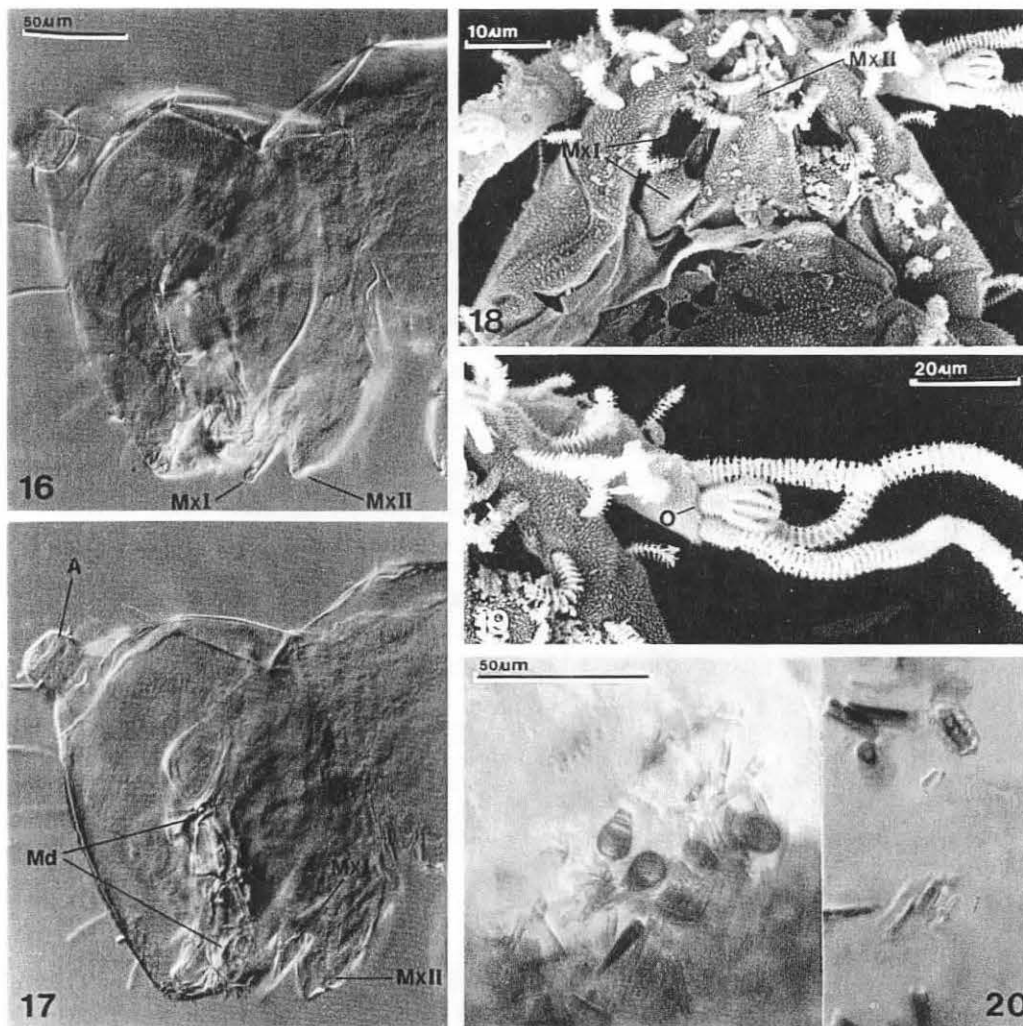
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Figs. 8-9: Symphyla gen. sp., ventral view of head with mandibles, maxillae I and maxillae II. VP refers to potential vestigium of palp.

Figs. 10-13: Diplopoda, *Polyxenus lagurus*. - 10) maxillae I and II from behind; 11) same, more obliquely from behind and below; in this view the distal parts of the mandibles become visible; 12) mandibles; 13) median semiglobular protuberances of mandibles, higher magnification.



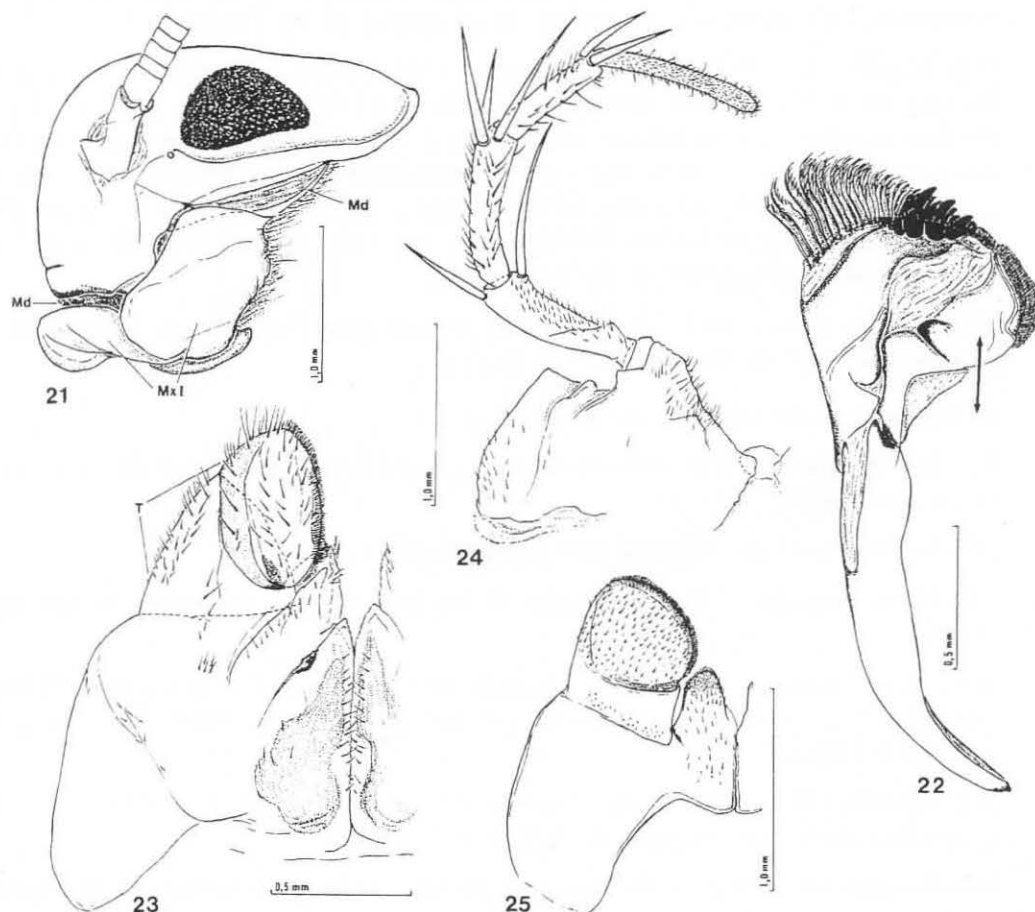
on the anterior position of the genital opening (progoneaty) as a character. But previous authors simply referred to progoneaty *as such* (see TIEGS 1940: 195). The (unpaired!) genital opening in the Symphyla is located on the IVth postcephalic sternite (between or shortly anterior to the to the base of the IVth pair of legs, i.e., *posterior* to the IIIrd pair of legs). At first glance, the situation in the Dignatha seems to be different. Paired genital openings are found on the tip of the so-called penes in males, and on the cyphopods of females. These structures occur posterior to the IIInd pair of legs. So the question arises of whether the special quality of progoneaty is different



Figs. 16-17: *Millotauropus silvestrii* REMY, 1953 (Symphyla, Hexamerocerata). - Head, lateral view, with large, segmented mandibles and tip of maxillae I (micrographs differ in focus levels).

Figs. 18-19: Brachypauropodidae gen. sp. - 18) Head, ventral view; 19) left antenna with "organe de candelabre", higher magnification.

20) *Millotauropus silvestrii*, remains of food in the midgut: broken fungal hyphae and conidia (Ascomycetes).



Figs. 21–25: *Scutigera coleoptrata* (Chilopoda, Notostigmophora). – 21) Head lateral view; 22) left mandible (arrow indicates direction of flexibility between distal part and long proximal trunk); 23) right maxilla I; 24) right maxilla II; 25) *Scolopendra* sp. (Chilopoda, Scolopendromorpha) right maxilla I.

in the Symphyla as opposed to the Dignatha. This is unlikely, however, for the following reason: The 1st pair of legs is reduced in the Dignatha. If one counts in a morphological sense, the genital opening *is* located posterior to the 3rd pair of legs. Accordingly, the genital openings occur at the same place in all progoneate taxa. This permits us to consider progoneaty as a sound autapomorphic character.

It could well be that penes and cyphopods, respectively, did not originate from nothing. Probably, they are homologues of an adequately transformed IVth pair of legs (counting morphologically) – at least in diplopods. Interpretations of this kind may be traced back to the early times of VERHOEFF (1901).

(14) Bothriotrichs<sup>4</sup>. – Somewhat superior but close to their base, the bothriotrichs of the Progoneata show a special enlargement which was called “bulbus” (HAUPT 1979;

<sup>4</sup> The term “Trichobothria” commonly used for these sense hairs curiously refers to the insertion (lat. →

see DOHLE 1980: 72 for review). Similar bothriotrichs are unknown from all other tracheates. This apparently is another autapomorphy of the Progoneata.

(15) Maxillae I. – With special reference to the Symphyla, various authors (e.g., HENNIG 1969: 81) mention that both maxillae I and II are lacking palps. As far as the first maxillae of symphyleans are concerned, this may not be true if the generally accepted homology of their segments is considered correct (cardo, stipes, galea, lacinia); a stout lateral cone may well represent a vestige of the palp. An alternative interpretation seems to be less probable. – In any case, we note “maxillae I without palps” as an autapomorphy of the Progoneata.

(16) Median eyes. – As in the chilopods, median eyes (“ocelli”) are reduced in all representatives of the Progoneata; see also (10).

a) *Symphyla as the adelphotaxon of the Dignatha*

The following selection of autapomorphies is listed here as proof for the monophyly of the Symphyla.

(17) Genital opening. – Genital opening unpaired (see (13)).

(18) Head spiracles. – One single pair of tracheal spiracles is located on the head capsule.

(19), (20) Reduction of all eyes. – Median eyes (19) as well as compound (lateral) eyes (20) were reduced independently of eye reductions in other taxa; they are completely lacking.

(21) Maxillae II. – The second maxillae are fused to form a functional labium; telopodites are lacking secondarily (Fig. 8–9, 26–27).

(22) Receptacula seminis. – Females have paired lateral spermathecae in their mouth cavity.

(23) Spinnerets. – Silk glands open at the tip of terminal paired spinnerets (“Spinngriffel”). These pieces (cerci?) have a special shape.

Note: We refer here to the special spinnerets of the Symphyla, and not to their ability *as such* to produce threads by paired silk glands that open terminally. This latter feature could be a character of the representatives of the stem lineage of all Labiophora or even of all Tracheata. Chilopods also produce silk threads when depositing spermatophores. For details see KAESTNER (1963: 1002).

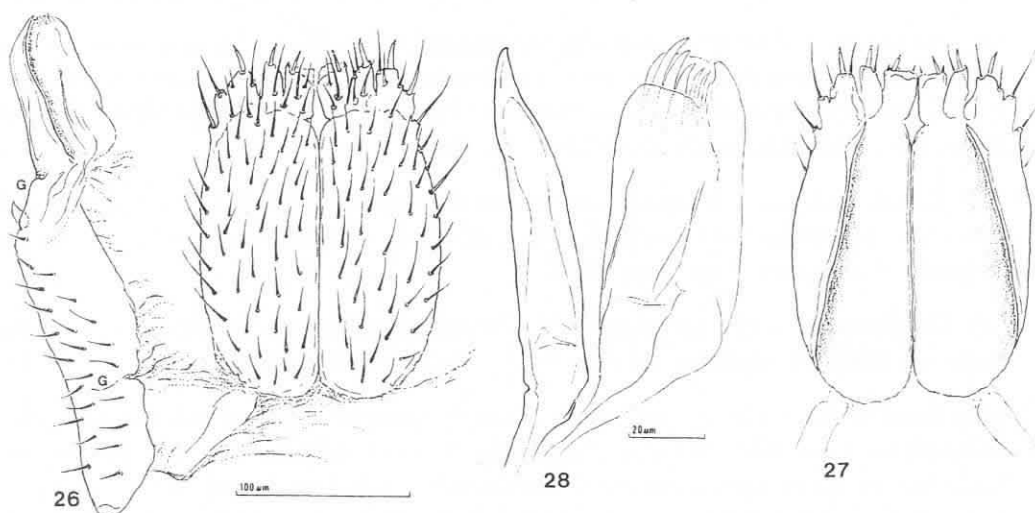
b) *Dignatha*

The Dignatha, adelphotaxon to the Symphyla, are characterized by the following autapomorphic features:

(24) Spiracles, tracheal pockets. – In the Dignatha, spiracles are located close to the base of the walking legs. Internally, they open into tracheal pockets. These simultaneously function as strong apodemes for part of the trunk musculature. This is an

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bothrium = cup), not to the sense hair (lat. trichius = hair) which is really meant. This is the reason why we use the term “bothriotrich”.



Figs. 26–28: *Symphyla* gen. sp. – 26) Maxilla II and right maxilla I somewhat removed, from below; 27) maxilla II from in front (= ventral border of mouth cavity); 28) distal part of maxilla I with “galea” and “lacinia”, higher magnification. – *VP* refers to potential vestigium of palp.

exquisite peculiarity and hence a sound autapomorphy of the taxon Dignatha. As far as pauropods are concerned, we remark that only representatives of their subtaxon Hexamerocerata maintained spiracles, tracheal pockets, and tracheae. There are still other plesiomorphic features, which were maintained only in the hexamerocerates (REMY 1953: 37).

Differences in the location of tracheal spiracles and in both structural and functional details of the tracheal systems in Hexapoda, Notostigmophora, all other Chilopoda, Symphyla and the Dignatha are striking. Any attempt to trace all this back to a single ancestral (pleurostigmophoran?) condition is a most daunting prospect. Therefore, we suspect that spiracles and tracheae evolved several times in the Tracheata (see (1)).

(25) Reduction of the 1st postcephalic pair of legs. – All authors share the view that the 1st postcephalic metamere (“collum segment”) has lost its appendages. As far as pauropods are concerned, as long ago as 1884 LATZEL (: 19) mentioned “auf der ventralen Seite (Kehle) ein rudimentäres Gliedmassenpaar” [a pair of vestigial limbs on the ventral (throat) side] and referred to his Fig. 12 [recte: 15] on Plate 2. These structures were called “exsertile vesicles” by TIEGS. He studied them in more detail (1947: 182, 249). In our view they represent vestiges of the first postcephalic pair of appendages.

(26) Penes. – All Dignatha share the presence of narrow, more or less pointed appendages behind the IIInd (morphologically 3rd) pair of legs. They are commonly called “penes” as they bear the male genital opening on the tip (see also (13)).

Note: The male genital opening was secondarily transferred to the base of the IIInd pair of walking legs in certain instances and the penes reduced, e.g., in the Polydesmoidea (Diplopoda).

b<sup>1</sup>) *The monophyly of the Pauropoda* is demonstrated, e.g., by the following characters:

(27) Antennae. – Pauropod antennae are primarily composed of 6 antennomeres. The penultimate antennomere bears one, the terminal two flagellae. Further, there is a special sensory organ of unknown function (Fig. 18–19, O); it was called “globulus” by LATZEL, and “organe de candelabre” by REMY.

(28) Coxal vesicles. – Exsertile vesicles on the ventral side of the 1st postcephalic metamere are unique to pauropods. They probably represent vestiges of the 1st pair of postcephalic appendages (see (25)).

(29) Pseudoculus. – The pseudoculus (“Schläfenorgan”) of the Pauropoda is a sensory organ of unknown function (HAUPT 1973). There are no complex eyes.

(30) Maxillae II. – The second maxillae simply form an unpaired subtriangular plate. Telepodites have been reduced completely in most subtaxa (Fig. 16–18). But two knob-like terminal appendages were maintained in the Eurypauropodidae (M. KRAUS, pers. observ.). They resemble to the paired interior “Taster” present in the gnathochilarium of chilognathous diplopods. We regard them to be vestiges of the telopodites of the 2nd maxillae – in the Pauropoda!

b<sup>2</sup>) *The monophyly of the Diplopoda*, adelphotaxon to the Pauropoda, can be demonstrated, e.g., by reference to the following autapomorphies:

(31) Diplopody. – Most recent authors still believe that the first postcephalic rings (“Thoracal-Segmente”) of diplopods are single metameres. This assumption is based mainly on results of embryological studies (DOHLE 1964, 1980). But VERHOEFF (1901, 1910–14: 40) assumed long ago that the first 4 postcephalic rings in question were diplosomites, – as were the succeeding ones. The problem was solved by KRAUS (1990). He demonstrated that VERHOEFF was right – even though diplosomites are hardly discernible in the anterior region of the trunk during the course of embryonic development. Accordingly, *all* postcephalic rings are diplosomites (the interpretation of the “collum segment” remains doubtful). This interpretation corresponds with ENGHOFF’s discovery (1993) of what he called “haplopody” in diplopods. The situation in the “Thoracal-Segmente” is interpreted here as persisting haplopody. This assumption is in harmony with the fact that no *anlagen* indicating the diplosomite nature of the anterior body rings are visible during the course of embryonic development (but see PFLUGFELDER 1932). – Diplopody in a strict sense is limited to the trunk from the 5th ring onwards.

(32) Antennae. – The distal segment of the antennae bears 4 sensory cones in all diplopods.

The Pselaphognatha (*Ps*) and the Chilognatha (*Ch*) differ as follows:

Compound eyes. – (33) Compound eyes reduced in *Ps* to single, isolated “ocelli”; each of them corresponds to an ommatidium. – (34) Compound eyes in *Ch* transformed into stemmata (see (9); SPIESS 1981).

Gnathochilarium. – (35) Maxillae II in *Ps* primarily with telopodites maintained (Fig. 10–11, 14–15); maxillae I located to some extent between the (anterior) mandibles and the (posterior) maxillae II (Fig. 11). – (36) Both maxillae fused in *Ch* to form the usual “complete” gnathochilarium (Fig. 4).

Cuticula. – (37) Cuticula of *Ps* soft and equipped with specialized setae, many grouped in tufts (Fig. 1d); last remaining bothriotrichia located on the vertex of the head capsule (see, e.g., EISENBEIS & WICHARD 1985 Pl. 68 Fig. c–d). – (38) Cuticula of *Ch* calcified; bothriotrichia are totally lacking.

## 2. Insecta (Hexapoda)

The monophyly of the insects is beyond all doubt (HENNIG, e.g., 1969, 1981). For this reason, we only mention a few autapomorphic key characters:

(39) Thorax. – The head capsule is followed by 3 thoracomeres bearing 3 pairs of locomotory appendages; (40) there are 11 abdominal metameres.

Outlines of the phylogenetic system of the insects have been presented and critically discussed in detail by HENNIG (1969, 1981). The reader is referred to his work. For this reason, we do not go into detail on the insect part of the argumentation scheme presented in Fig. 2. Basic characters are as follows:

(41) Entognathy; (42) antennae composed of three antennomeres, the distal one annulated; (43) dicondyl of the mandibles; this functionally includes cooperation with the first maxillae and hence should be understood as a functional complex.

We maintain the view that Hexapoda is a synonym for Insecta. There is no reason to separate the Collembola from the other “true” insects. This was proposed by KUKALOVÁ-PECK (1987): She classified a taxon Hexapoda into Parainsecta (with the Collembola) and Insecta (for all other hexapod taxa). However, it may well be that the Diplura will prove to be a paraphyletic unit. There is evidence that the Japygina make up the adelphotaxon to all remaining Entognatha, with the Campodeina as adelphotaxon to Protura + Collembola (see BILIŃSKI & SZKLARZEWICZ 1992).

## E. Phylogenetic age and primary food niches

Crustacea were already present in the Lower Cambrian (BRIGGS et al. 1993; WHATLEY et al. 1993). Consequently, the same minimum age must be inferred for the Tracheata. The first Diplopoda are known from Late Silurian and Early Devonian deposits (ALMOND 1985; ROSS & BRIGGS 1993). Almost “modern” Chilopoda were found at the Middle Devonian (Givet) Gilboa site: *Devonobius delta* SHEAR & BONAMO, 1988. JERAM et al. (1990) report remains of a presumptive notostigmophoran (i.e., a scutigeromorph centipede) of the Upper Silurian. *Rhyniella praecursor* HIRST & MAULIK,



1926 (Collembola), the oldest hitherto known insect, is of Lower Devonian age. This implies that the corresponding adelphotaxa are at least equal in age (*arrows* in Fig. 2).

This relative sequence of phylogenetic branching indicates that the origin of the higher subtaxa of the Tracheata can be traced back to Cambrian and early Silurian times.

SHEAR & KUKALOVÁ-PECK (1990) used the fossil evidence for an analysis of the ecology of palaeozoic terrestrial arthropods. They conclude that herbivory – the direct consumption of living plant materials – “may have been rare in early Paleozoic ecosystems”, and continue “that most primary productivity was funneled through detritivores and decomposers”.

In contrast to this approach, we will start with an analysis of the main food niches of the Recent representatives of the various higher tracheate taxa. Then we will try to relate feeding habits of today with what was presumably available for terrestrial arthropods in Late Cambrian and Early Silurian times. – The following information is taken from the literature, mainly from KAESTNER (1963, 1973).

Symphyla feed on soft tissue plants and on the smallest rootlets of young plants, but also on small arthropods. As far as is known, pauropods suck out fungal hyphae. Crunched plant materials, especially of fungi, including conidia, have only been observed in the gut of Hexamerocerata (Fig. 20). Colobognatha (Diplopoda-Chilognatha) also suck out fungal hyphae; a special kind of entognathy was developed in such genera as *Polyzonium* and *Siphonophora* as a functional adaptation to this food niche. *Polyxenus* (Diplopoda-Pselaphognatha) feeds on unicellular algae. The distal teeth of the mandibles (Fig. 12) are used for removal of the algae from the surface; they are then squashed between special projections on the median side of these mouthparts (Fig. 13). Archaeognatha feed in a similar way and also have semiglobuliform projections on the median side of the mandibles (Fig. 6). The gut of specimens of the *Zygentoma* contained remains of unicellular algae, fungal spores and ‘detritus’. Japygina are of minor interest in this analysis as they are predators. But Campodeina (e.g., *Campodea*) feed on fungal hyphae and ‘detritus’. Protura are also known to suck out fungal hyphae. Even the diet of the Collembola (secondarily macrophagous forms excluded) is similar to the spectrum reported here (see KAESTNER 1973: 302); semiglobuliform projections on the mandibles may also be present.

In general, the representatives of nearly all higher taxa under discussion drill holes into plant cells and suck out the contents *or* are able to damage cell walls in order to get at and digest the contents. The same principle of drilling a hole and sucking out living cells has been developed by terrestrial Tardigrada (Pararthropoda) (see KAESTNER 1969: 596). Could it be that more massive cell walls were primarily developed as a means of protection against sucking and squeezing/crushing?

The tracheates discussed here apparently maintained archaic – i.e., plesiomorphic – food niches that have existed since early Palaeozoic times. Primary resources of this kind continue to be available. We postulate that they have been continuously in use over hundreds of million years. In our view, this explains the wide distribution of entognathy (Entognatha, Colobognatha) as well as of different stages of semiento-



gnathy<sup>5</sup> (Pauropoda, Symphyla, Pselaphognatha). This is functionally correlated with means of damaging cell walls located on the median side of the mandibles (Pselaphognatha, Collembola part., Archaeognatha part.).

But which other groups were successful in forming *new*, more advanced food niches? We mention the Chilognatha among diplopods (the Colobognatha excepted) on the one side<sup>6</sup> and many but far from all groups of the Pterygota on the other. Potential exceptions are the Zoraptera, Psocoptera, and the Thysanoptera. Within narrow limits, acquisition of new niches happened also in those Collembola that are secondarily macrophageous.

Remarkably, this increase of body size happened in the very groups of tracheates that successfully produced the greatest amount of diversity. This seems to be correlated with the evolution of more effective digestion mechanisms, e.g., oesophageal crops, symbiotic systems such as mycetomes etc. Unfortunately, little is known about the digestive mechanisms of the Chilognatha among diplopods, but there is evidence that masses of intestinal Bacteria and other microorganisms may play a major role (CRAWFORD 1988; for review see HOPKIN & READ 1992: 54–58).

The parallel increase of body size in the Chilopoda (up to 26.5 cm length: *Scolopendra* sp.) and also in certain Recent and fossil Japygids (up to 58 mm: *Japyx gallardi* TILLYARD, 1924; *Testajapyx thomasi* KUKALOVÁ-PECK, 1987, Upper Carboniferous) is regarded as less problematical as the representatives of both groups are predators<sup>7</sup>.

In conclusion, we suspect that the ancestral tracheate was a remarkably small arthropod with a body length of between 1 and 2 mm. This implies that the trunk was composed of a limited number of metameres only. This is in conformity with the situation present in the Symphyla, Pauropoda, Pselaphognatha, and Insecta. In the ground pattern of the Chilopoda, the original number of leg-bearing postcephalic metameres was similarly low (16) (BORUCKI, pers. commun.). This supports the view that high or even extremely high numbers of trunk metameres (up to more than 182 leg-bearing metameres in the Geophilomorpha; similar figures in the Iulida among diplopods) are due to a secondary increase according to the "elongation theory" (see HOPKIN & READ 1992 for review).

<sup>5</sup> We use the term "semientognathy" to designate those mouthparts which are characterized by a broad, laterally expanded clypeolabrum; the effect of this is that the mandibles are scarcely visible from outside (Pauropoda: Fig. 14–16; Pselaphognatha: Fig. 11). Further, the first maxillae tighten the mouth cavity laterally (Symphyla: Fig. 9; Pselaphognatha: Fig. 11).

<sup>6</sup> We also refer to the extinct Arthropleurida inc. sed. of the Upper Carboniferous, which were up to 180 mm long. Arthropleurids are conventionally regarded as myriapodomorphs, but one cannot exclude the possibility that they were not tracheates. Remains of lycopod epidermis and tracheid cells have been found as food remains in fossil specimens. As they were apparently able to feed directly on living plant materials, the same correlation with increased body size can be stated; but nothing is known of how they were able to digest this kind of diet.

<sup>7</sup> *Ramsdelepidion schusteri* KUKALOVÁ-PECK, 1987, was assigned to the Zygentoma. If this were true, this fossil of the Upper Carboniferous would have been a giant silverfish, with a body length of 6 cm. But this assignment does not yet seem to be definitive: so far, only drawings (reconstructions) of the animal have been published and no detailed description.

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## Abbreviations:

<i>G</i>	Articulation between segments
<i>IP</i>	Intermaxillary plate
<i>K</i>	Maxillipedes ("Kieferfüße")
<i>Md</i>	Mandible
<i>Mx I</i>	Maxilla I
<i>Mx II</i>	Maxilla II
<i>O</i>	Organe de candelabre (globulus)
<i>P</i>	Duct of the "Putzdrüse"
<i>S</i>	Stipes
<i>T</i>	Telopodite
<i>VP</i>	Vestigial palp?

## F. Literature

Citations have not been provided for general information as such facts can be found in relevant textbooks.

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